PAN-PACIFIC ENTOMOLOGIST
65(3), 1989, pp. 322–347

Late Quaternary and Modern Arthropods from the Ajo Mountains of Southwestern Arizona

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Abstract.—Fossil and modern arthropods were studied in the Ajo Mountains of Organ Pipe Cactus National Monument, Pima County, Arizona. A total of 203 arthropod taxa were collected in rocky desertscrub habitats in Alamo Canyon using various techniques. Five species were new for Arizona; six were significant range extensions. This typical Sonoran Desert fauna has strong affinities to the southwestern United States (53.6%) and Mexico (49.3%), especially the Baja California Peninsula (29.0%), with a number of Arizona endemics (13.8%).

Excluding contaminants, 54 arthropod taxa in 26 genera and 16 species were identified from 10 fossil packrat (*Neotoma* sp.) middens ranging in age from 32,000 to 1150 yr B.P. from 915 to 975 m elevation in the Ajo Mountains. About 70–85% of the taxa potentially occur in Alamo Canyon today although the estimates are high due to identifications to relatively high taxonomic levels. The arthropods of ice age woodlands in cool, wet climates were a mixture of extralocal and local species. Some of the extralocals survived well into the Holocene postglacial while others expanded their ranges during a relatively recent (1150 yr B.P.) wet period. Generally distributional changes in response to glacial climates were similar in arthropods and plants. However, the ranges of the long lived trees, shrubs, and succulents were much more dynamic and changes in community structure and composition in the plant communities were more easily seen due to species identifications and detailed knowledge of the local flora.

Well-preserved plant remains from ancient packrat (*Neotoma* sp.) middens have played an important role in reconstructing the history of vegetation and climate in the deserts of North America (Van Devender et al., 1987). Faunal remains are less common than those of plants but are associated with floral assemblages and radiocarbon dates. Small vertebrate remains from packrat middens have been studied for some areas including the Sonoran Desert in Arizona and California (Mead et al., 1983; Van Devender and Mead, 1978).

Packrat middens are an exciting new source of fossil arthropods. In the Chihuahuan Desert a few arthropod remains were reported in middens from the Big Bend of Texas (Ashworth, 1973) and the Fra Cristobal Mountains, New Mexico (Elias, 1987). Others were reported from Sonoran Desert middens including the tenebrionid *Stibia tuckeri* Casey (a darkling beetle) from a 14,400-yr B.P. (radiocarbon years before 1950) sample from the Kofa Mountains of Arizona (Ashworth, 1976; Morgan et al., 1983). *Ptinus priminidi* Spilman (Ptinidae), was described from middle and late Wisconsin middens from the Whipple Mountains of California, and the Artillery and Kofa mountains of Arizona (Spilman, 1976). Hall et al. (1988) presented fossil records of 50 arthropod taxa from 41 fossil packrat middens from 160 to 625 m elevation in the Tinajas Altas and Butler mountains of Arizona and the Hornaday Mountains and Sierra del Rosario of northwestern Sonora. Hall et al. (1990) summarized fossil records for 43 arthropod taxa from a 14,120-yr chronological series of 21 samples from 550 to 605 m elevation from the Puerto Blanco Mountains in Organ Pipe Cactus National Monument, Arizona. In this paper we present the arthropod remains from 10 packrat middens from two higher areas in the Ajo Mountains in the Monument.

Sonoran Desert.—The Sonoran Desert is the arid and semi-arid subtropical area centered around the head of the Gulf of California in western Sonora, southwestern Arizona, southeastern California, and much of the Baja California Peninsula (Shreve, 1964; Fig. 1). Elevations range from below sea level in the Salton Sea Basin in California to about 1000 m in Arizona (Turner and Brown, 1982). All portions of the Sonoran Desert may occasionally experience freezing temperatures although the duration is rarely more than a single night. Rainfall along an east–west gradient changes from a biseasonal regime with strong summer monsoons in the eastern Sonoran Desert to a winter rainfall regime in Baja California and in the Mohave Desert in California. The hottest, driest North American deserts are in the Lower Colorado River Valley in Arizona and California (Cole, 1986) and the Gran Desierto of northwestern Sonora (Ezcurra and Rodrigues, 1986; Felger, 1980).

Organ Pipe Cactus National Monument is a unique area in southwestern Arizona where a suite of subtropical Sonoran Desert plants including *Stenocereus thurberi* (Engelm.) Gibson and Horak (organ pipe cactus), *Sapium biloculare* (Wats.) Pax. (Mexican jumping bean), and *Jatropha cinerea* (Ort.) Muell. and *J. cuneata* Wiggins and Rollins (limber bushes) enter the United States (Bowers, 1980). Shreve (1964) proposed formal subdivisions of the Sonoran Desert which were refined by Turner and Brown (1982). The lower elevations in Organ Pipe including the Puerto Blanco Mountains midden sites at 550–605 m support Lower Colorado River Valley desertscrub communities. Dominants include *Cercidium microphyllum* (Torr.) Rose and Johnst. (foothills palo verde), *Encelia farinosa* Gray (brittlebush), *S. biloculare,* and *S. thurberi* (Van Devender, 1987; Hall et al., press).

The Ajo Mountains rise to 1465 m elevation and support sparse chaparral/relict woodland and desert-grassland. The Montezuma's Head site is at 975 m on a steep west-facing slope just above the *Stenocereus thurberi* communities of the Arizona Upland. A single *Juniperus erythrocarpa* Cory (redberry juniper) is near the rockshelter. The Alamo Canyon site at 915 m is on an east-facing slope in a steep, rough mountain canyon. *Stenocereus thurberi* is abundant with occasional *Carnegiea gigantea* (Engelm.) B. and R. (saguaro) and a relatively dense subtropical scrub dominated by *Simmondsia chinensis* (Link) Schneid. (jojoba), *Coursetia glandulosa* Gray (samo prieto), *Ambrosia cordifolia* (Gray) Payne (Sonoran bursage), and *Dodonaea viscosa* Jacq. (hop bush). The lowest woodland plants including *Juniperus erythrocarpa, Quercus ajoensis* C. H. Muell. (Ajo oak), and *Vauquelinia californica* (Torr.) Sarg. (Arizona rosewood) are just up canyon.

Vegetation history.—The history of vegetation and climate for the last 40,000

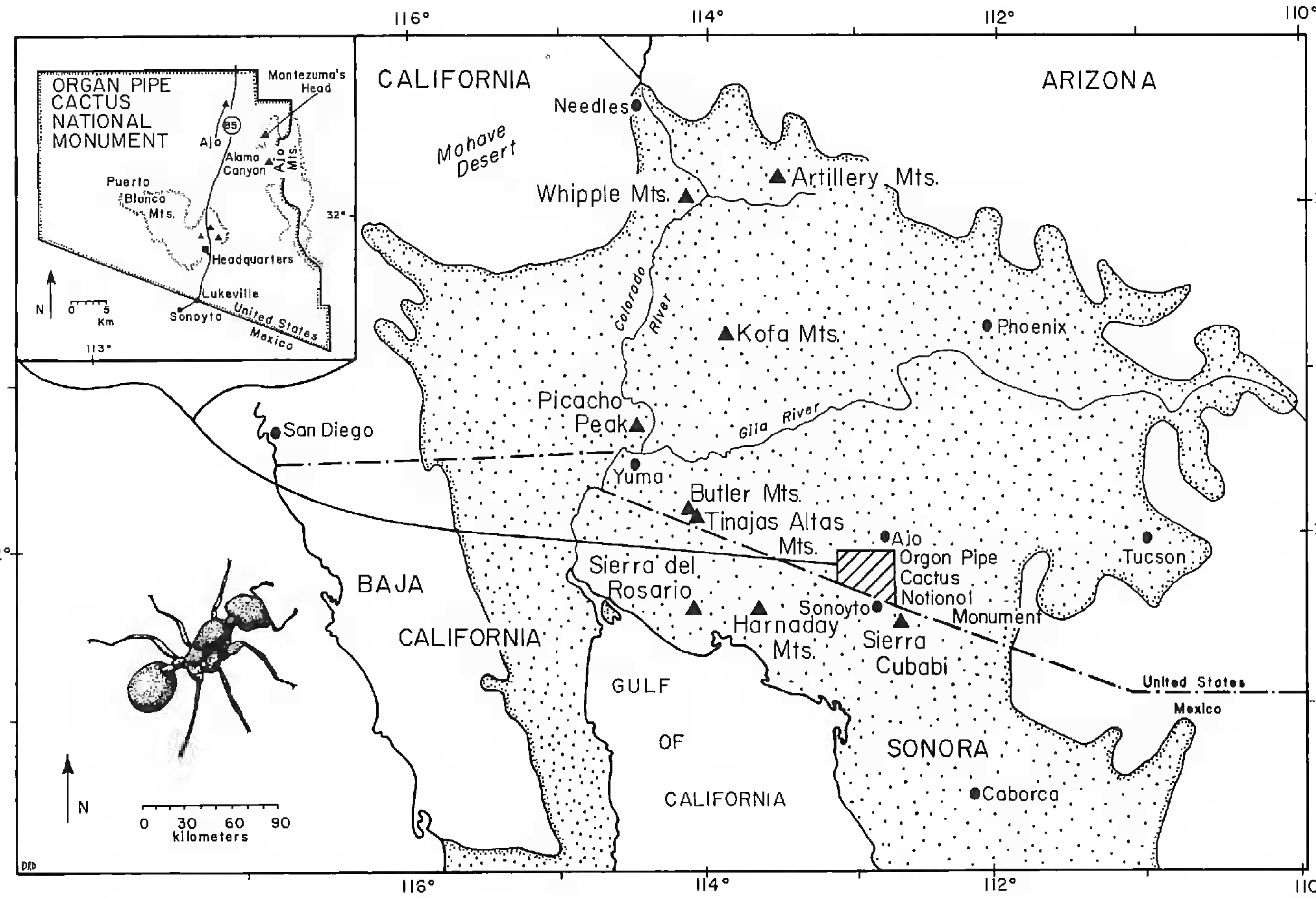

Figure 1. Map of area discussed in text. Sonoran Desert in stipple after Shreve (1964). Solid triangles = packrat midden site. Ant = *Pogonomyrmex barbatus* Smith (harvester ant).

yr has been reconstructed using plant macrofossils in packrat middens from the Sonoran Desert in Arizona and California (Van Devender, 1987; Van Devender et al., 1987). Organ Pipe Cactus National Monument has an exceptionally good packrat midden record. A series of 21 samples from 535 to 605 m elevation provide a record of the vegetation in the Puerto Blanco Mountains for the last 14,120 yr B.P. (Van Devender, 1987). A late Wisconsin California juniper–Joshua tree woodland was displaced by a relict woodland dominated by *Encelia farinosa* and *Acacia greggii* Gray (catclaw), with low levels of *Juniperus californica* and *Carnegiea gigantea* by 10,540 yr B.P. in the early Holocene. In the middle Holocene (8900–4000 yr B.P.), *E. farinosa* and *C. gigantea* grew on hot south-facing slopes with riparian trees and shrubs. The modern vegetation was established by about 4000 yr B.P. as *A. greggii, Cercidium floridum* Benth. (blue palo verde), and *Prosopis velutina* Woot. (velvet mesquite) were restricted to nearby washes and *C. microphyllum* and *Stenocereus thurberi* arrived in the area. The present vegetation and climate are as hot and dry as at any time in the record.

Ten packrat middens from Montezuma's Head and in Alamo Canyon provide a record of the vegetation for 915–975 m elevation in the nearby Ajo Mountains for the last 32,000 yr B.P. (Table 1). Plant remains in the Wisconsin samples record a mesic pinyon-juniper-oak woodland with *Pinus monophylla* Torr. & Frem. (single leaf pinyon), *Juniperus scopulorum* Sarg. (Rocky Mountain juniper), *Quercus ajoensis, Artemisia tridentata* Nutt.-type (big sagebrush), and *Yucca brevifolia* Engelm. (Joshua tree) from 32,000 to at least 13,500 yr B.P. A xeric woodland with *J. californica* Carr. (California juniper), *J. erythrocarpa,* and *Q. ajoensis* was present from 9585 to 8130 yr B.P. *Carnegiea gigantea* was present in these early Holocene woodlands although *Stenocereus thurberi* is much more common in the

Table 1. Radiocarbon ages for packrat middens yielding arthropods from 915 m elevation in Alamo Canyon (AC) and 975 m on Montezuma's Head (MH) in the Ajo Mountains, Pima County, Arizona.

Sample	Age (yr B.P.)	Lab. no.	Material dated	Paleovegetation
AC 2C	32,000 ± 4400	A-2119	*Juniperus* spp. twigs, seeds	pinyon-juniper-oak woodland
AC 2X	29,110 ± 1100	A-4985	*Neotoma* sp. fecal pellets	pinyon-juniper-oak woodland
MH 1B	21,840 ± 650	A-1696	*Pinus monophylla* needles	pinyon-juniper-oak woodland
MH 1A	20,490 ± 510	A-1695	*Juniperus* spp. twigs, seeds	pinyon-juniper-oak woodland
AC 1B	14,500 ± 300	A-2120	*Juniperus* spp. twigs, seeds	pinyon-juniper-oak woodland
MH 1D	13,500 ± 390	A-1698	*Juniperus* spp. twigs, seeds	pinyon-juniper-oak woodland
AC 1U	9910 ± 210	A-2211	*Quercus ajoensis* acorns, leaves	juniper-oak woodland
	9230 ± 370	AA-533	*Carnegiea gigantea* seeds	
	9570 ± 180	av. A-2211 & AA-533		
AC 1A1	8590 ± 470	AA-539	*Carnegiea gigantea* seeds	oak-juniper chaparral
AC 1A2	8130 ± 370	A-2209	*Neotoma* sp. fecal pellets	oak-juniper chaparral
	8130 ± 430	AA-540	*Carnegiea gigantea* seeds	
	8130 ± 280	av. A-2209 & AA-540		
AC 3	1150 ± 240	A-2120	*Juniperus erythrocarpa* twigs, seeds	Sonoran desertscrub/chaparral

area today. The rich floral assemblage in the 1150 yr B.P. sample from Alamo Canyon reflects the modern desertscrub near an isolated *J. erythrocarpa* although increased species richness probably indicates relatively greater rainfall than today.

Methods

Packrat middens are hard, shiny organic deposits that are preserved in dry rockshelters. Well-preserved plant fossils are excellent for radiocarbon dating allowing samples from local areas to be arranged in chronological sequences. Arthropod fossils from the Ajo Mountains middens were identified through comparison with reference specimens in the University of Arizona Entomological Collection (UAZ) and will be deposited there.

Taphonomy.—Twigs, leaves, and fruits are collected by packrats within about 30 m of the rockshelters. Animal remains in the middens are mixtures of materials collected by the packrats, other rockshelter residents, and material transported to the rockshelter by predators. Most of the arthropod specimens found in midden samples are fragments of resident ground dwellers such as tenebrionid beetles, scorpions, and ants. Ryckman et al. (1981) provided a comprehensive bibliography of the commensals and parasites of *Neotoma,* including arthropods like the kissing bug (*Triatoma* spp., Reduviidae).

Although packrats have generalized diets and take animal protein on occasion, they are primarily herbivores and probably did not collect many of the midden arthropods, especially the very small ones, for food. We have seen occasional small fragments of beetle elytra inside *Neotoma* fecal pellets. Some arthropods were probably carried to the middens as adults on plant material collected by the packrat or as larvae within branches that emerged later. When packrats urinate on a midden or humidity in the air increases during rains, the surface can become a sticky trap for smaller residents. The abundance and relative completeness of spider beetles (Ptinidae) in the samples may be due to this process.

Another source of arthropod remains in middens may be from the regurgitated pellets of raptorial birds or the scat of small mammalian predators such as *Bassariscus astutus* (Lichtenstein) (ringtail), *Spilogale gracilis* (Linnaeus) (spotted skunk), or *Mephitis* spp. (skunks). As pellets or scat disintegrate arthropod fragments can be incorporated into the accumulating midden. Arthropod remains from these sources may reflect greater sampling areas than more locally derived material. Arthropod predators such as spiders may account for some of the specimens as well. We have seen a web of *Lactrodectus hesperus* Chamberlain and Ivie (black widow spider) festooned with bee and fly carcasses hanging over a fossil midden in a rockshelter in the Waterman Mountains in the northeastern Sonoran Desert.

By no means do the midden arthropods represent adequate samples of the local fauna or reflect their relative abundances. Some arthropods, especially millipedes, can leave behind numerous recognizable fragments from a single individual (Table 2). Although the taphonomic processes that lead to the deposition of arthropods in middens are poorly known, the processes and any biases in the samples can be assumed to have been relatively constant.

Contamination.—The hardness of the middens, saturation with urine and plant chemicals, and lack of visible signs of burrowing suggest that most of the arthropod remains are primary and not intrusive. Plant contaminants from younger outer

Table 2. Numbers of arthropods identified from fossil packrat middens from the Ajo Mountains, Pima County, Arizona. Ages in thousands of years follow Table 1.

Taxa	Material	32.0	29.1	21.8	20.5	14.5	13.5	9.6	8.6	8.1	1.2
Arachnida (spiders, scorpions, mites, ticks)											
Acarina (ticks)											
Family indet.	body										1
Araneae (spiders)											
Salticidae (jumping spiders)											
Genus indet.	cephalothorax							1			1
Chelonethida (pseudoscorpions)											
Family indet.	body fragments			11	4		12				23
Scorpionida (scorpions)											
Vejovidae											
Vejovis sp. (stripe tailed scorpion)	tail segments						2				
Family indet.	telson, tail segments	1	1		2	2	4				
Diplopoda (millipedes)											
Lysiopetalidae (crested millipedes)											
Genus indet.	segment fragments				1		1				5
Family indet.	segment fragments	1	3			2	3	5			
Insecta (insects)											
Coleoptera (beetles)											
Bruchidae (bean weevils)											
Algarobius prosopis (LeConte)	body									1[1]	
Stator limbatus (Horn)	elytra								1		1
Genus indet.	elytra							1			2
Buprestidae (metallic wood boring beetles)											
Agrilus sp.	abdominal segment									1	
Carabidae (ground beetles)											
Genus indet.	head, elytra			2	4		3	4			
Cerambycidae (long-horned beetles)											
Genus indet.	tarsal segments					1					1

Table 2. Continued.

Taxa	Material	32.0	29.1	21.8	20.5	14.5	13.5	9.6	8.6	8.1	1.2
Chrysomelidae (leaf beetles)											
Cf. *Glyptina* (flea beetle)	bodies				1		1				
Genus indet.	elytron				1						
Curculionidae (weevils)											
Conotrachelus sp.	head				2						
Eucyllus echinus Van Dyke	body			1							
Cf. *Tychius*	body			1							
Smicronyx sp. (marsh weevils)	body	1									
Genus indet.	body, legs		1		3	3	4				
Dermestidae (carpet beetles)											
Genus indet.	larval skin, body			2[1]	2[1]		2[1]				3[1]
Elateridae (click beetles)											
Genus indet.	pronotum							2			
Melyridae (soft winged flower beetles)											
Genus indet.	larva			1							
Ptinidae (spider beetles)											
Niptus nr. *abtrusus* Spilman	bodies							17	4	1	24
Niptus sp.	body fragments	13	22			7		6		3	5
Ptinus feminalis Fall	body fragments				5						13
Ptinus cf. *fur* (Linnaeus)	bodies and fragments	1		20	4		36				15
Salpingidae (narrow waisted bark beetles)											
Cononotus bryanti Van Dyke	head					1					
Scarabaeidae (scarabs)											
Aphodius sp.	head, elytron						2[1]				
Onthophagus cf. *brevifrons* Horn (dung beetle)	head							1			
Onthophagus velutinus Horn (dung beetle)	body					1				1	2
Genus indet.	misc. fragments					2		3			1
Scolytidae (bark & ambrosia beetles)											
Cactopinus hubbardi Schwarz (saguaro bark beetle)	body								1	1	
Tenebrionidae (darkling beetles)											
Argoporis sp.	legs					1	1				
Genus indet.	legs	1		5	4	6	3	2			5

Table 2. Continued.

Taxa	Material	32.0	29.1	21.8	20.5	14.5	13.5	9.6	8.6	8.1	1.2
Dictyoptera (termites, roaches, mantids)											
Polyphagidae (cockroaches)											
Arenivaga sp. (desert roach)	tibia, leg fragments				1	2					20
Diptera (flies)											
Stratiomyidae											
Genus indet.	larva										1
Family indet.	pupal bodies, puparia		3	1	2	2	40		1	1	
Hemiptera (true bugs)											
Cydnidae (burrowing bugs)											
Dallasiellus californicus (Blatchley)	pronotum										1
Genus indet.	head										1
Lygaeidae (seed bugs)											
Nysius raphanus Howard (chinch bug)	bodies				1[1]		1[1]				
Genus indet.	body fragments							1			113
Scutelleridae (shield back bugs)											
Acantholomida porosa (Germar)	sternum										1
Homoptera (leaf & tree hoppers)											
Cicadae (cicadas)											
Genus indet.	femur-tibia										2
Membracidae (tree hoppers)											
Micrutalis sp.	pronotum			1							
Hymenoptera (ants, bees, wasps)											
Formicidae (ants)											
Aphaenogaster boulderensis Smith	heads										3
Aphaenogster sp.	head			6	5		15	1			
Crematogaster sp.	bodies, wings	2		2			1		10	3	
Liometopum sp.	heads					3					
Neivamyrmex nigrescens (Cresson)	head, thorax		2					1	1		1
Pheidole sp.	heads								1		1
Solenopsis aurea Wheeler	body fragments	2					1				18
Trachymyrmex arizonensis (Wheeler)	body		1					4	1		1
Genus indet.	heads, bodies				3	2	6				

Table 2. Continued.

Taxa	Material	32.0	29.1	21.8	20.5	14.5	13.5	9.6	8.6	8.1	1.2
Sphecidae (sphecid wasps)											
Genus indet.	head							1			1
Lepidoptera (moths, butterflies)											
Family indet.	pupa, body			1[1]	1			1			
Siphonoptera (fleas)											
Dolichopsyllidae											
Orchopeas sexdentatus Baker (flea)	body										1
Totals: No. specimens: 678	22	22	33	54	46	35	138	51	20	12	267
No. taxa: 57	8	8	7	13	16	14	18	16	8	8	29

[1] Probable contaminant.

layers are usually very small percentages of the total number of identified specimens. Arthropod fossils are at least an order of magnitude less common than the plant fossils. Rare arthropod contaminants may be incorporated into the midden in the same manner although we have not observed it.

In the present study arthropod contaminants were from a different source. When the midden samples were disaggregated in water they were not covered and insects attracted to lights fell in. These specimens were readily recognized because they retained some of their original colors and shiny surfaces and were not impregnated with the amber-colored urine of the midden matrix. Obvious contaminants flagged in Table 2 include *Aphodius* sp. (a scarab beetle), *Algarobius prosopis* (LeConte) (a seed weevil), larval skins of dermestids (carpet beetles), an adult moth, and *Nysius raphanus* Howard (a chinch bug). The dermestid remains were probably debris from colonies of *Dermestes* sp. maintained to clean vertebrate skeletons.

Modern arthropods.—The arthropod fauna of Alamo Canyon was sampled monthly from March to November of 1987 using several collection techniques (Table 3). Specimens were deposited into the collections at UAZ and Organ Pipe Cactus National Monument. Unfortunately the sampling was in a year of extreme heat and little rainfall in both the winter–spring and summer rainy seasons. Although the list in Table 3 is impressive, it probably represents a small portion of the normal fauna.

Ten pitfall traps (covered plastic cups with 90–100 mm diameter top) containing ethylene glycol were used to sample the fauna at 915–975 m on steep rocky slopes near the packrat midden rockshelter in the north fork of Alamo Canyon from March to September (ca. 300 trap nights per month for 6 mo). Pitfall traps are very effective at sampling ground dwelling animals, including rare and extremely secretive species. Additional arthropods were collected in leaf litter from near packrat den entrances in upper Alamo Canyon using a Berlese funnel trap, from plants throughout the area using beat sheets and sweep nets, and using a black light at night from 730 m in the mouth of Alamo Canyon.

Arthropod Fauna

The pitfall traps in Alamo Canyon provided good samples of the ground dwelling fauna. A number of species collected in the traps have been reported in the literature as living in packrat houses or dens including *Ptinus agnathus* Fall, *P. feminalis* Fall (spider beetles), *Onthophagus velutinus* Horn (a dung beetle), *Trox carinatus* Loomis, *T. inflatus* Loomis (scarab beetles), *Nidicola marginata* Harris and Drake, and *Triatoma rubida* (Uhler) (kissing bug). From this study and Hall et al. (1988, 1990), *Cononotus bryanti* Van Dyke (narrow waisted bark beetle), a scalpingid beetle endemic to Arizona, must have close ties to packrat dens.

Due to the accumulation of organic material near and in the packrat houses, the pitfall traps yielded a bounty of tenebrionid detritivores including significant Arizona range extensions for *Anepsius delicatulus* LeConte, *Asidina wickhami* Horn, *Cryptoglossa angularis* Horn, *Eleodes wickhami* Horn, and *Stibia tuckeri*. *Stibia tuckeri* was previously known from the type specimens from near Tucson (Casey, 1924), the Puerto Blanco Mountains (Hall et al., 1990), and a 14,400 yr B.P. packrat midden from the Kofa Mountains (Morgan et al., 1983).

A number of specimens in the pitfall traps are new additions to the Arizona

Table 3. Collections and observations of arthropods from March to November of 1987 in Alamo Canyon, Ajo Mountains, Pima County, Arizona. Abbreviations: States of United States follow U.S. Postal Service two-digit code; AG—Argentina, BC—Baja California, BCN—Baja California del Norte, BCS—Baja California del Sur, CH—Chihuahua, CU—Coahuila, DU—Durango, EC—Ecuador, GU—Guatemala, HO—Honduras, JA—Jalisco, MR—Mississippi River, MX—Mexico, NI—Nicaragua, NL—Nueva Leon, OA—Oaxaca, RM—Rocky Mountains, SI—Sinaloa, SO—Sonora, US—United States, VC—Vera Cruz, VZ—Venezuela, WS—Widespread; e—eastern, n—northern, s—southern, sw—southwestern, w—western.

	Taxa	Geographical distribution
Class Arachnida		
Order Araneae		
Family Loxoscelidae	*Loxosceles* sp.	
Family Therophosidae	*Aphonopelma* sp.	
Order Scorpionida	*Vejovis* sp.	
Class Chilopoda	*Scolopendra heros* Girard	AZ, sCA, MX
	Scutigera sp.	
Class Diplopoda		
Order Spirostreptida		
Family Spirostreptidae	*Orthoporus ornatus* (Girard)	swUS deserts
Order Polyxenida		
Family Polyxenidae	*Polyxenus* sp.	Rare
Class Insecta		
Order Coleoptera		
Family Anthicidae	*Ischyropalpus* sp.	
Family Bruchidae	*Algarobius prosopis* (LeConte)	TX–MX (BC)
	Mimosestes amicus (Horn)	TX–MX (SO, BC)
	Stator limbatus (Horn)	TX–CA, MX
Family Buprestidae	*Agrilus impexus* Horn	
Family Cantharidae	*Chauliognathus obscurus* Schaeffer	AZ
Family Carabidae	*Amara* sp.	
	Apenes sp.	
	Cicindela lemniscata LeConte	TX–AZ, MX (DU, CH, SO, BCS)
	Colliuris pennsylvanica (Linnaeus)	
	Discoderus sp.	
	Harpalus oblitus LeConte	CO, NM, AZ
	Lebia arizonica Shaeffer	AZ
	Pinacodera punctigera (LeConte)	TX–CA
	Pterostichus arizonicus Schaeffer	AZ
	Selenophorus sp.	
	Tetragonoderus fasciatus Haldeman	WS
Family Cerambycidae	*Aneflomorpha* sp.	
	Derobrachus geminatus LeConte	TX, AZ, MX (BCS)
	Methia mormona Linell	CO, UT, NM, AZ
	Moneilema gigas LeConte	TX–AZ, UT, MX
	Stenelaphus alienus (LeConte)	AZ, MX
	Sternidius centralis LeConte	
Family Chrysomelidae	*Coscinoptera aeneipennis* LeConte	TX, AZ, MX (BCS)
	Pachybrachys snowi Bowditch	AZ
	Pachybrachys xanti Crotch	AZ, MX (BCS)
	Pachybrachys spp.	
Family Cleridae	*Cymatodera antennata* Schaeffer	swUS, nMX
	Cymatodera delicatula Fall	swUS, nMX

Table 3. Continued.

Taxa		Geographical distribution
	Cymatodera sp.	
	Enoclerus quadrisignatus Say	
Family Curculionidae	*Apion ventricosum* LeConte	CO, UT, TX–CA, MX (BC)
	Microtychius simplex (Casey)	TX–AZ, MX
	Microtychius transversus (Casey)	TX–CA, NV, UT, MX (BC)
	Ophryastes varius LeConte	
	Pandeleteinus lucidillus A. Howden	AZ, MX (BC)
Family Dascillidae	*Amecocerus* sp.	
Family Elateridae	*Conoderus ferruginosus* Fall	AZ, MX
	Dicrepidius corvinus Candeze	
	Eniconyx sp.	
	Esthesopus parcus Horn	AZ
	Neotrichophorus arizonensis (Schaeffer)	AZ
Family Histeridae	*Xerosaprinus* sp.	
Family Lathridiidae	*Akalyptoischion atrichos* Andrews	AZ, CA
Family Meloidae	*Epicauta tenella* (LeConte)	NV, NM–CA, MX (SO, CH, DU, BCS)
	Epicauta tenuilineata (Horn)	AZ–CA, MX (SO, BCS)
Family Mordellidae	*Pentaria pallida* (Liljebald)	KS, CO, TX–CA
	Mordellistena ambusta LeConte	WS
Family Nitidulidae	*Carpophilus dimidiatus* (Fabricius)	WS, Temperate & Tropical
Family Oedemeridae	*Oxacis laevicollis* Horn	
	Oxacis matthewi Arnett	
	Oxacis sp.	
Family Ostomidae	*Temnochila aerea* (LeConte)	NM–AZ, MX (BC), HO
Family Pedilidae	*Duboisus arizonensis* (Champion)	AZ
Family Ptinidae	*Ptinus agnatus* Fall	AZ, sCA
	Ptinus feminalis Fall	AZ
Family Salpingidae	*Cononotus bryanti* Van Dyke	AZ
Family Scaphidiidae	*Baeocera* sp.	
Family Scarabaeidae	*Ataenius desertus* Horn	UT, AZ–CA, BCS
	Ataenius hirsutus Horn	
	Diplotaxis knausii Schaeffer	swUS, MX (BC)
	Diplotaxis morens LeConte	swUS, MX (BC)
	Diplotaxis subangulata Schaeffer	swUS, MX (BC)
	Onthophagus velutinus Horn	TX, AZ, CO, MX (BCS)
	Oxygrilius ruginasus (LeConte)	NM–CA, MX (SO, BC)
	Phileurus illatus LeConte	AZ, MX (BC), EC, VZ
	Phyllophaga lenis (Horn)	AZ, sCA
	Phyllophaga timida (Horn)	AZ
	Trox carinatus Loomis	eAZ–TX, MX (CH)
	Trox inflatus Loomis	eAZ–TX, MX (CH)
	Trox punctatus Germar	MR–CA, MX (BC)
Family Staphylinidae	*Xenomedon* sp.	
Family Tenebrionidae	*Anepsius delicatulus* LeConte	AZ–CA, MX (nSO, BC)
	Argoporus alutacea Casey	AZ, CA, MX (SO)
	Asidina wickhami Horn	AZ
	Blapstinus castaneus Casey	TX–AZ, CO
	Centrioptera variolosa Horn	AZ, MX (BC)
	Conibius opacus (LeConte)	AZ, CA

Table 3. Continued.

Taxa		Geographical distribution
	Cryptoglossa angularis Horn	AZ, CA, MX (BC)
	Doliodesmus charlesi Spilman	
	Eleodes carbonaria (Say)	TX–AZ
	Eleodes debilis LeConte	TX–AZ
	Eleodes subnitens LeConte	AZ
	Eleodes wickhami Horn	NM–AZ
	Eusattus reticulatus (Say)	
	Hylocrinus oblongulus Casey	
	Hymenorus sp.	AZ, CA, MX (BC)
	Metoponium sp.	
	Nocibiotes granulatus (LeConte)	AZ–CA, MX (BC)
	Platydema inquilinum Linell	AZ
	Stibia tuckeri Casey	AZ
	Triorophus histrio Casey	AZ
	Typhlusechus chemehuevii Aalbu and Andrews	AZ, CA
Order Dictyoptera		
Family Kalotermitidae	*Marginitermes hubbardi* (Banks)	
Family Mantidae	*Yersiniops solitarium* (Scudder)	RM–AZ
Family Polyphagidae	*Arenivaga* sp.	
Family Rhinotermitidae	*Heterotermes aureus* (Snyder)	AZ, CA
Family Termitidae	*Amitermes snyderi* Light	AZ–CA (Mohave & Sonoran deserts)
	Gnathamitermes perplexus (Banks)	TX–CA
Order Diptera		
Family Asilidae	*Efferia* spp.	
Family Bombyliidae	*Lordotus perplexus* Johnson and Johnson	
	Phthiria sp.	
Family Syrphidae	*Volucella isabellina* Williston	NM–AZ, MX (SO)
Family Tephritidae	*Euaresta* sp.	
Order Hemiptera		
Family Anthocoridae	*Nidicola marginata* Harris and Drake	AZ, CA
Family Coreidae	*Leptoglossus brevirostris* Barber	
	Mozena arizonensis Ruckes	AZ
	Narnia sp.	
Family Cydnidae	*Dallasiellus californicus* (Blachley)	NM–CA, MX (BCN)
	Melanaethus subglaber (Walker)	TX–CA, UT, MX (SO, BC)
	Pangaeus bilineatus (Say)	WS
	Pangaeus setosus Froeschner	TX, AZ, MX
Family Largidae	*Largus cinctus* (Herrich-Schaeffer)	swUS
Family Lygaeidae	*Exptochiomera oblonga* (Stal)	swUS
	Ligyrocoris nitidulus Uhler	
	Ligyrocoris sp.	
	Lygaeus rubricollis Uhler	swUS
Family Miridae	*Phytocoris vanduzeei* Reuter	NM, NV, AZ, CA
Family Nepidae	*Ranatra quadridentata* Stal	swUS
Family Notonectidae	*Buenoa arizonensis* Bare	AZ
	Notonecta kirbyi Hungerford	ND–TX–CA
Family Pentatomidae	*Brochymena parva* Ruckes	swUS
	Dendrocoris contaminatus Uhler	TX–CA, UT
	Thyanta pallidovirens Ruckes	wUS

Table 3. Continued.

Taxa		Geographical distribution
Family Phymatidae	*Macrocephalus dorannae* Evans	swUS
Family Reduviidae	*Apiomerus longispinnis* Champion	swUS
	Melanolestes abdominalis Evans	WS
	Rhiginia cinctiventris Stal	TX–AZ
	Sinea confusa Caudell	swUS
	Triatoma rubida (Uhler)	TX–CA, MX (VC, SI, SO, BC)
	Zelus socius (Uhler)	
Family Scutelleridae	*Camirus moestus* (Stal)	AZ, MX (OA, JA)
Order Homoptera		
Family Cercopidae	*Clastoptera arizonana* Doering	AZ
Family Cicadellidae	*Draeculacephala portola* Doering	
	Phlepsanus vanduzeei (Ball)	
	Scaphytopius sp.	
	Xestocephalus sp.	
Family Cixiidae	*Oecleus* sp.	
	Oliarus complectus Ball	
Family Fulgoridae	*Scolops* sp.	
Family Issidae	*Hysteropterum cornutum* Melichar	CO–UT, AZ–CA
Family Membracidae	*Campylenchia latipes* (Say)	WS
	Centrodontus atlas paucivenosus Cook	NM–CA, UT
	Multareis cornutus lawsoni Cook	AZ, CA, UT
	Mutareoides bifurcata Cook	
Family Psyllidae	*Aphalaroida* sp.	
	Leuronota maculata (Crawford)	TX, AZ
Order Hymenoptera		
Family Andrenidae	*Perdita* sp.	
Family Braconidae	*Agathis nigripes* (Cresson)	WS
Family Chrysididae	*Chrysis* sp.	
Family Formicidae	*Aphaenogaster cockerelli* (Andre)	TX–sCA, MX
	Camponotus sp.	
	Crematogaster sp.	
	Cyphomyrmex rimosus (Spinola)	FL–CA, MX–AG
	Neivamyrmex nigrescens (Cresson)	TX–SC, MX (SO, BC)
	Odontomachus clarus Roger	TX, NM, AZ, SCA, MX (NL, DU, CU, CH, SO, BC)
	Pheidole vistana Forel	AZ, sCA, MX
	Pseudomyrmex apache Creighton	sTX–sCA, MX
	Solenopsis aurea Wheeler	wTX–sCA, MX
Family Mutillidae	*Dasymutilla magnifica* Mickel	NM–CA, MX (BC)
Family Pompilidae	*Agenioideus birkmanni* (Banks)	US–MX (OA)
	Aporinellus sp.	
	Auplopus mexicanus (Cresson)	AZ, MX (VC)
	Pepsis chrysothemis Lucas	TX–CA, MX (SO, BC)
	Pepsis formosa (Say)	NM–CA, MX (SO, BC)
Family Tiphiidae	*Aglyptacros* sp.	AZ
	Brachycistis sp.	
	Tiphia sp.	
Family Vespidae	*Polistes flavus* Cresson	CO–NV, NM–CA, MX (SO)

Table 3. Continued.

Taxa		Geographical distribution
Order Lepidoptera		
Family Noctuidae	*Erastroideas propera* Grote	
	Hemeroplanis sp.	
	Melipotis indomita Walker	
	Tarachida clausula (Grote)	
	Cactobrosis fernaldialis (Hulst)	AZ, CA
Family Pyralidae	*Noctuelia* sp.	
Family Sphingidae	*Manduca sexta* (Linnaeus)	MD, NY–FL, MA–sCA
Order Neuroptera		
Family Mantispidae	*Plega* sp.	
Family Myrmeleontidae	*Brachynemurus yavapai* Currie	AZ, UT, MX (BC)
	Eremoleon nigribasis Banks	AZ, NM, UT, MX (BC)
	Vella hesperus Banks	AZ, NM, MX (BC)
Order Odonata		
Family Libellulidae	*Libellula saturata* Uhler	MO, KS, OK, ID, WY, CO, UT, NV, TX–CA, MX (NL, CU, CH, SO, BC)
	Pseudoleon superbum Hagen	swUS–GU
	Sympetrum corruptum Hagen	WS
Order Orthoptera		
Family Acrididae	*Encoptolophus subgracilis* Caudell	swUS, MX, HO
	Leprus intermedius Saussure	TX–CA, CO–UT, MX (BC)
	Ligurotettix coquilletti Caudell	NV, AZ, CA, MX (SO, BC)
	Poecilotettix pantherinus (Walker)	AZ, MX (SO)
	Psoloessa texana Scudder	NB–TX–CA, MX (BC)
	Schistocerca vaga (Scudder)	TX–CA, MX–NI
	Trimerotropis pallidipennis (Burmeister)	wUS, MX (BC)
Family Gryllidae	*Gryllus assimilis* (Fabricius)	WS
Family Tettigoniidae	*Arethaea gracilipes papago* Hebard	AZ, CA
	Atelopus schwarzi Caudell	sAZ
	Insara elegans Scudder	wTX–AZ, MX
Family Phasmidae	*Pseudosermyle straminea* Scudder	TX, CO–CA
Order Thysanura		
Family Machilidae	*Machilis* sp.	

arthropod fauna including *Hylocrinus oblongulus* Casey and *Typhlusechus chemehuevii* Aalbu and Andrews (tenebrionid beetles), *Hysteropterum cornutum* Melichor (an issid homopteran), and *Pheidole vistana* Forel (a myrmecine ant). *Typhlusechus chemehuevii* is a tiny flightless, nearly blind beetle previously only known from the Providence Mountains of California (Aalbu and Andrews, 1985).

The Berlese funnel trap yielded the lathridiid beetle *Akalyptoischion atrichos* Andrews and the relatively unknown millipede *Polyxenus* from litter samples. *Akalyptoischion atrichos* is a recently described genus and species (Andrews, 1976). It is a fungus and detritus feeder previously known from various habitats from montane forests to coastal chaparral to Mohave desertscrub in California.

Orthoporus ornatus (Girard) (desert millipede) is very common in Alamo Canyon. Our observation of it grazing on new leaves of *Coursetia glandulosa* a meter off the ground has apparently not been previously reported for this widespread detritivore (Wooten and Crawford, 1975).

Blacklighting in Alamo Canyon to sample the nocturnal aerial fauna was not very productive due to relatively low insect populations in a dry year. However alates of a rare termite, *Amitermes snyderi* Light, were taken. They were flying in association with the more common *Gnathamitermes perplexus* (Banks), a behavioral situation that may explain why the alate form has not been described in the literature (Nutting, 1969).

Examination of the distribution patterns of Alamo Canyon arthropods in Table 3 is enlightening. The largest groups are species that are widespread in the southwestern United States (53.6%) and also found in some portion of Mexico (49.3%). Forty of the Mexican species (29.0%) occur on the Baja California Peninsula. In this study of buprestid beetles Van Dyke (1942) previously pointed out close ties between the arthropod faunas of Sonora and Baja California, especially Baja California del Sur, and the mainland Sonoran Desert in Sonora, Arizona, and California. Although Sonoran distributions were not as clearly identified, the border is only 24 km to the south; undoubtedly many Alamo Canyon arthropods also occur there.

Six or seven of 21 species of tenebrionid beetles collected in Alamo Canyon were common. The remainder probably represent less common species with low populations or transients. Thomas (1983) reached similar conclusions in his extensive study of tenebrionid beetles in the eastern Mohave Desert in southern Nevada and northwestern Arizona: i.e., a nucleus of common species and a number of transients. The steep, rocky slopes in our Alamo Canyon study area do not tend to accumulate litter in comparison with gentler alluvial bajadas or relatively flat areas in valleys. Low litter availability limits the number of desert detritivores, especially of flightless tenebrionids, in permanent residency. The vagility of these insects helps account for the many apparent transients.

Ten species in the Alamo Canyon fauna (7.2%) only enter the United States in Arizona with eight more (5.8%) also reaching southern California. Nineteen species (13.8%) are only known from Arizona. An additional 10 species only known from Arizona and California brings the total of regional endemics to 21.0%.

Arthropod History

A total of 57 arthropod taxa representing 13 orders, 27 families, 29 genera, and 18 species was identified from the 10 packrat midden samples from the Ajo Mountains (Fig. 2; Tables 1, 2). A total of 678 specimens was identified with 12–267 (ave. 67.8) specimens and 7–29 (av. 13.7) taxa per sample. The contaminants (two species, a genus, and a family) discussed above were not included in calculations of percentages and similarity indices on the fauna. The results are presented in summary chronological diagrams (Figs. 3, 4). In general ground dwelling groups such as scorpions, pseudoscorpions, millipedes, beetles, and ants make up the bulk of the fauna. The most common beetle families are the Ptinidae and Tenebrionidae with good representation for the Bruchidae, Carabidae, Curcu-

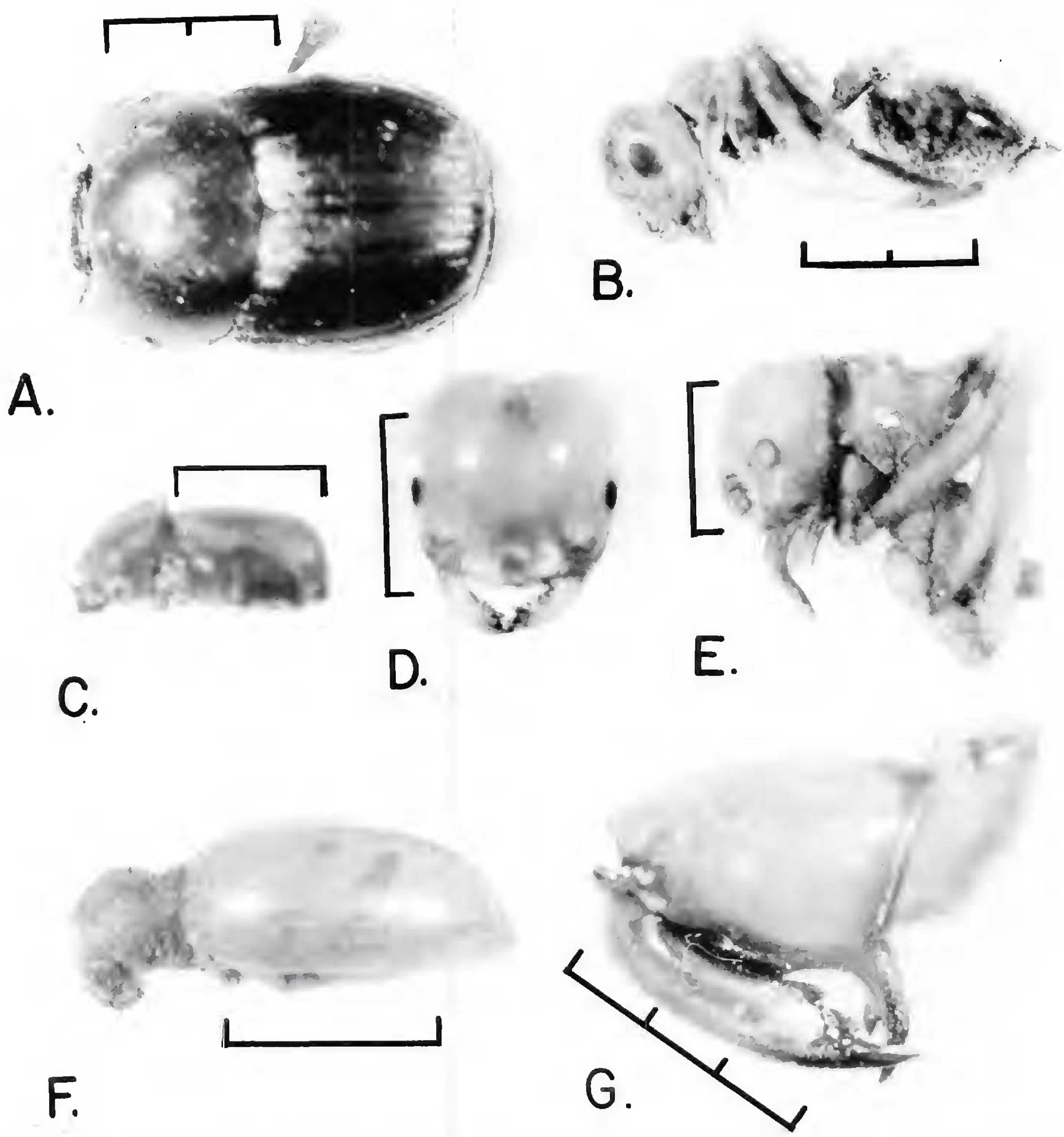

Figure 2. Fossil insect remains from Ajo Mountains packrat middens, Pima County, Arizona. Scale divisions in millimeters. A. *Onthophagus velutinus* (Scarabaeidae) body (14,500 yr B.P.). B. *Crematogaster* sp. (Formicidae) body (9585 yr B.P.). C. *Cactopinus hubbardi* (Scolytidae) body (9585 yr B.P.). D. *Solenopsis aurea* (Formicidae) head (1150 yr B.P.; also E–G). E. *Trachymyrmex arizonensis* (Formicidae) head to petiole. F. *Ptinus* nr. *fur* (Ptinidae) body. G. Cicada (Cicadidae) foreleg of nymph.

lionidae, and Scarabaeidae. With seven genera, the ants are the most diverse group sampled. Indeterminant remains of fly larvae and pupae were surprisingly common.

Local species.—A number of the taxa identified from the Ajo Mountains middens still live in Alamo Canyon (Table 3). The ants *Crematogastor* sp., *Neivamyrmex nigrescens* (Cresson), and *Solenopsis aurea* Wheeler have been present since the middle Wisconsin (32,000–29,110 yr B.P.). Arthropods that first appeared in the record in the late Wisconsin (21,840–13,500 yr B.P.) include *Aphaenogaster* sp., *Arenivaga* sp., *Cononotus bryanti, Onthophagus velutinus, Ptinus*

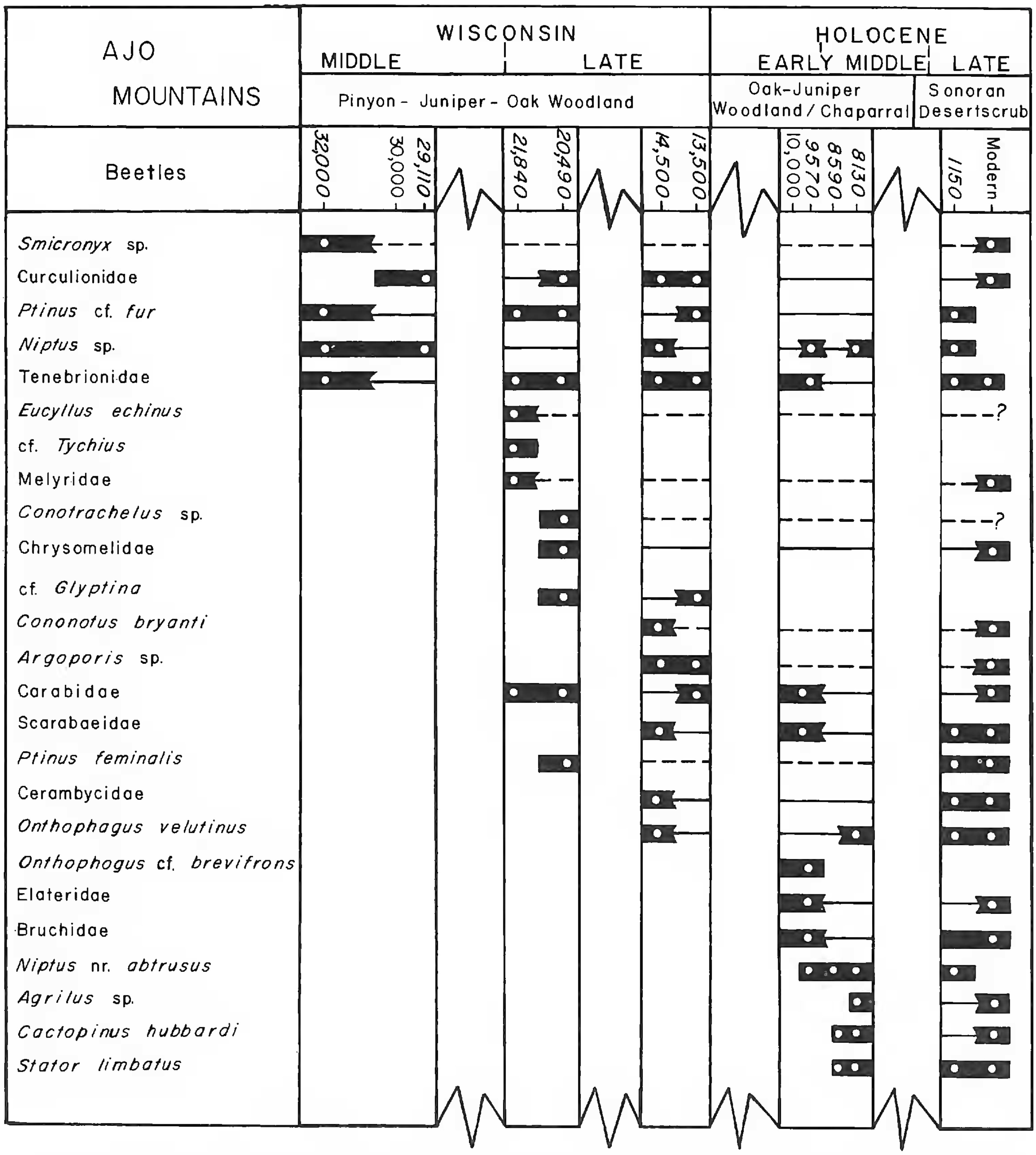

Figure 3. Chronological summary of fossil beetles recovered from Ajo Mountains packrat middens.

feminalis, and *Vejovis* sp. *Agrilus* sp., *Cactopinus hubbardi* Schwarz, *Pheidole* sp., and *Stator limbatus* (Horn) appeared in middle Holocene (8590–8130 yr B.P.) samples. This early record of *Cactopinus hubbardi* (the saguaro bark beetle, Scolytidae) reflects the arrival of its host, *Carnegiea gigantea* (Van Devender, 1987). Although *C. hubbardi* is not common today and difficult to collect, it is a regular fossil in the middens. The fossils of *C. gigantea* are mostly seeds and not pieces of the rotting tissue inhabited by the beetles. Relatively complete bodies of *C. hubbardi* suggest that they were trapped on sticky midden surfaces. *Cactopinus hubbardi* may leave the cacti and use the rockshelters for part of the year. Potential leguminous hosts for *Stator limbatus* (Bruchidae) in the samples were *Acacia*

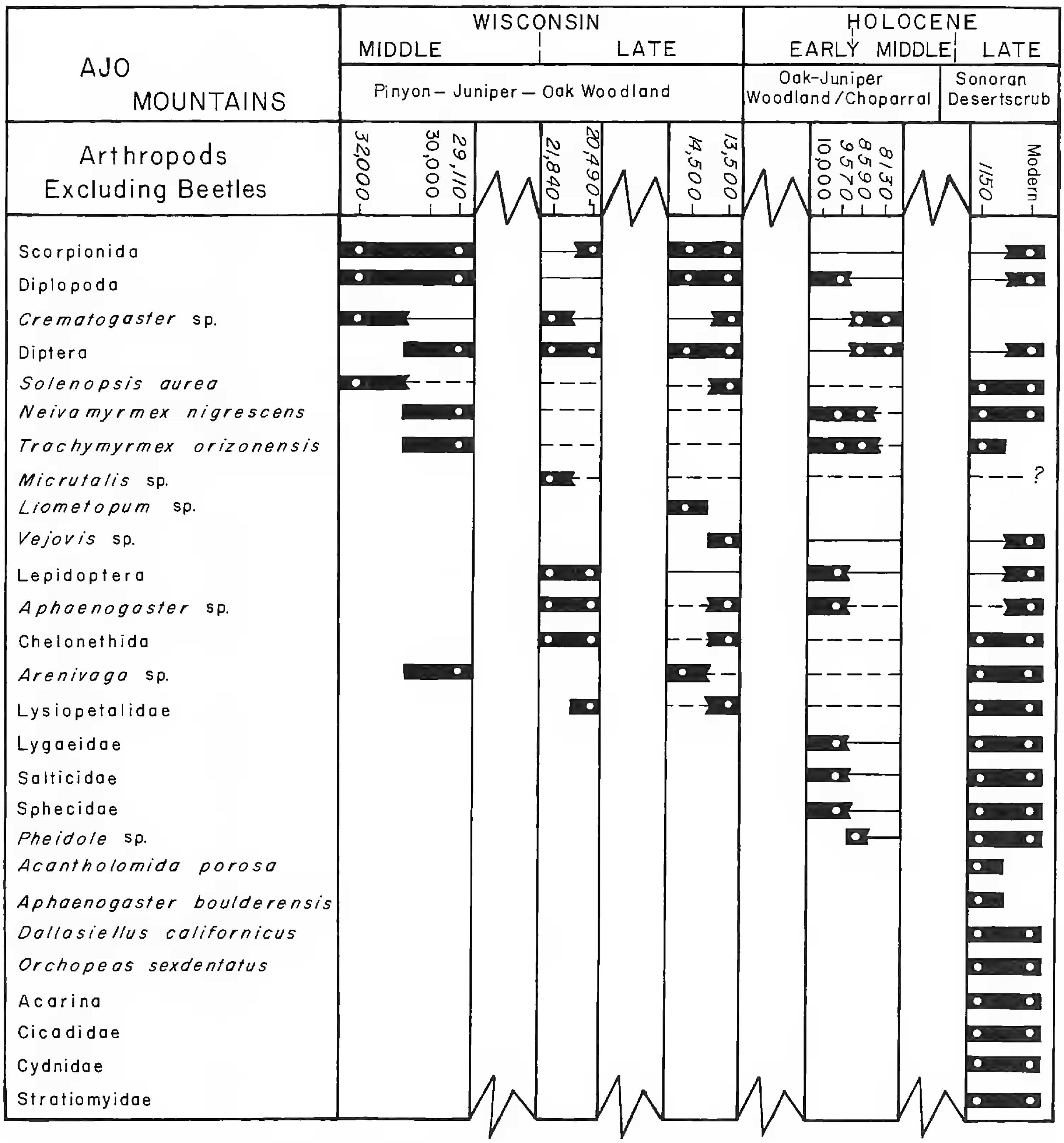

Figure 4. Chronological summary of fossil arthropods exclusive of beetles from Ajo Mountains packrat middens.

greggii and *Prosopis velutina. Dallasiellus californicus* (Blatchley) (a burrowing bug, Cydnidae) was identified from the late Holocene (1150 yr B.P.) sample.

Extralocal species.—Sixteen arthropods (30.2%) identified from packrat midden specimens that were not collected in Alamo Canyon have differing significances. Several weevils were found in the middle and late Wisconsin (32,000–21,840 yr B.P.) pinyon-juniper samples. Specimens in UAZ indicate that *Conotrachelus* sp., *Eucyllus echinus* Van Dyke, and *Smicronyx* sp. are widespread in Sonoran desertscrub and would not be surprising if found in the Ajo Mountains. A specimen of *E. echinus* from "Organ Pipe Park" may be from the Monument. *Smicronyx* sp. occurs in the Puerto Blanco Mountains (Hall et al., 1990). However, cf. *Tychius* apparently represents a woodland species that presently lives above the desert.

The UAZ specimens of *T. prolixus* Casey are from 1710 m elevation in Snowflake, Arizona (355 km NE) and San Diego, California.

Spider beetles are common commensals in packrat houses that are often found in packrat middens. A total of 196 specimens (28.9%) in four taxa were found in the Ajo Mountains samples. *Niptus abtrusus* Spilman is a cave dwelling species known from Val Verde and Brewster counties of eastern Trans-Pecos Texas and adjacent Coahuila, Mexico (Spilman, 1968). It was previously reported from a 12,000 yr B.P. packrat midden from Maravillas Canyon Cave, Texas (Ashworth, 1973). Although this species is closely related to *N. ventriculus* LeConte of Arizona, the fossils appear closer to *N. abtrusus* using Spilman's (1968) key and comparative specimens. *Niptus* cf. *ventriculus* was reported in late Holocene (1910 and 130 yr B.P.) samples from the Puerto Blanco Mountains but has not been collected in recent arthropod surveys in the Monument. Although the midden records of *N.* nr. *abtrusus* indicate a major range extension of a Chihuahuan Desert beetle to the Ajo Mountains, its abundance in Holocene (9585–1150 yr B.P.) samples suggests it may eventually be collected in Arizona. The genus *Niptus* appears to have been more common in the study area for the last 32,000 yr than it is today.

Ptinus nr. *fur* (Linnaeus) was found in late Wisconsin (21,800 and 13,500 yr B.P.) and late Holocene (1150 yr B.P.) samples. Although this beetle has a cosmopolitan distribution (Papp, 1962), the only Arizona specimens in UAZ are from Globe and Phoenix. In the 20,490 and 1150 yr B.P. samples, it was associated with *P. feminalis. Ptinus feminalis* was previously found in pitfall traps and eight late Holocene (3480–30 yr B.P.) middens in the Puerto Blanco Mountains (Hall et al., 1990).

Several arthropods were only found in late Wisconsin samples. The melyrid beetle and the tree hopper *Micrutalis* sp. (Membracidae) are widespread and may occur in the Ajos. The melyrid specimen was a larva which is carnivorous or scavenges on animal materials (White, 1983). However, the ant *Liometopum* sp. in the 14,500-yr B.P. sample and the flea beetle cf. *Glyptina* (Chrysomelidae) in the 13,500-yr B.P. sample probably reflect the cooler, moister climates of glacial times.

Liometopum is a genus of ants that nest in soil beneath cover or under bark or in crevices in trees in the mountains of the southwestern United States (Krombein et al., 1979). *Liometopum luctuosum* Wheeler lives at 1370–2470 m elevation in pinyon-juniper woodland or higher conifer forests in Nevada (Wheeler and Wheeler, 1986). This species and *L. apiculatum* Mayr have been taken from a number of localities at 1070–2290 m elevation in the mountains of southeastern and central Arizona, often in woodland or chaparral. Only a specimen of *L. luctuosum* from Safford is from a desert elevation (890 m) but could reflect a mesic microhabitat in an urban setting. The nearest records for both species to the midden site are in the Santa Catalina Mountains (115 km ENE).

At least four species of *Glyptina* occur in Arizona in various habitats up to cool, moist high mountain areas in the eastern half of the state (UAZ specimens). *Glyptina atriventris* Horn enters the upper edge of the Sonoran in the Tucson and Safford areas although the specimens may be from more mesic urban or agricultural settings. The nearest locality to the Ajo Mountains for *Glyptina* sp. is from desertscrub in the Waterman Mountains (130 km ENE).

Trachymyrmex arizonensis (Wheeler) was identified from a middle Wisconsin

(29,110 yr B.P.) and three Holocene (9570–1150 yr B.P.) samples. Today this montane ant is only known from relatively mesic habitats in the Huachuca and Santa Rita mountains of southeastern Arizona.

Segment fragments of tiny crested millipedes (Lysiopetalidae) were found in late Wisconsin (20,490 and 13,500 yr B.P.) and late Holocene (1150 yr B.P.) samples. Specimens of this secretive form from the Puerto Blanco Mountains (Hall et al., 1990) suggest that it probably occurs in the Ajo Mountains as well.

The specimen of *Onthophagus* cf. *brevifrons* Horn in the 9585-yr B.P. sample is of special interest. This rare dung beetle is only known in Arizona from the Chiricahua Mountains and near the Pinal Mountains (210 km NE) in packrat houses (Howden and Cartwright, 1963). These localities are either at the upper edge of desert-grassland, in Mexican pine-oak woodland, or interior chaparral. Elias (1987) also reported it from two late Holocene (3420–4340 yr B.P.) packrat middens from 1705 m elevation in Rhodes Canyon in the San Andres Mountains of south-central New Mexico. The middens contained plant remains of the modern Chihuahuan desertscrub/desert-grassland vegetation.

The remaining midden taxa not known from the Ajo Mountains (*Acantholomida porosa* (Germar), *Aphaenogaster boulderensis* Smith, *Orchopeas sexdentatus* Baker, and a stratiomyid fly) were from the 1150-yr B.P. sample. *O. sexdentatus* is a widespread flea that has been collected on packrats in Arizona including *Neotoma lepida* Thomas (desert packrat) in Organ Pipe and *N. albigula* Hartley (white throated packrat) in Tucson (UAZ specimens). One or both of these two species probably constructed the fossil middens. Stratiomyids probably occur in Organ Pipe as well.

Acantholomida porosa is widespread in the United States from Virginia to Oregon and Florida to California (Lattin, 1964). Arizona specimens in UAZ are from relatively mesic habitats in the Pinaleño, Santa Catalina, and Atascosa mountains. *Aphaenogaster boulderensis* is known from western Texas to southern Nevada and southern California (Wheeler and Wheeler, 1986). The only Arizona specimens in UAZ are from Horseshoe Island in Lake Mead and the Grand Canyon, over 400 km to the north-northwest of Alamo Canyon.

Thus, the actual number of extralocal species in the midden fauna may be only eight (15.1%). The presence in the youngest sample of species presently known from the Chihuahuan Desert in Texas and Coahuila (*Niptus abtrusus*) or from widespread localities in the Southwest but rare in Arizona (*Aphaenogaster boulderensis, Ptinus* cf. *fur*), or from relatively mesic habitats in mountains with Sierra Madrean affinities in southeastern Arizona (*Acantholomida porosa, Trachymyrmex arizonensis*) is interesting. The wealth of arthropods in the 1150 yr B.P. sample (267 specimens and 29 taxa), and especially of pseudoscorpions (23 specimens) and ptinids (57 specimens in four taxa), indicate relatively mesic conditions for Sonoran desertscrub. Plant macrofossils in the Puerto Blanco Mountains also recorded a very wet period at about the same time (980 and 990 yr B.P.; Van Devender, 1987). The significance of these apparent range extensions is difficult to assess because of inadequate knowledge of the arthropod fauna of the Ajo Mountains and many other areas in the Sonoran Desert. Were *Niptus abtrusus, Ptinus fur,* and *Trachymyrmex arizonensis* survivors from wetter periods in the Late Wisconsin and Holocene that were only recently extirpated? Did *Acantholomida porosa* and *Aphaenogaster bouldernesis* temporarily expand their ranges

Table 4. Comparison of the Ajo Mountains midden arthropod fauna with similar faunas from the Puerto Blanco (Hall et al., in press), Tinajas Altas, Butler, and Hornaday (Hall et al., 1988) mountains. Sorenson's index of similarity (S.I.) is calculated by 2C/A + B (C = shared taxa between samples, A and B = sample totals).

Site	No. speci-mens	Total taxa				Families				Genera			
		No.	C	%	S.I.	No.	C	%	S.I.	No.	C	%	S.I.
Ajo Mts.	678	53	—	—	—	31	—	—	—	30	—	—	—
Puerto Blanco Mts.	715	43	22	51.2	0.46	30	17	56.7	0.56	25	10	40.0	0.36
Tinajas Altas Mts.	357	32	15	46.9	0.35	21	14	66.7	0.54	15	4	26.7	0.18
Butler Mts.	65	17	9	52.9	0.26	12	8	66.7	0.37	7	2	28.6	0.11
Hornaday Mts.	218	23	16	69.6	0.42	18	13	72.2	0.53	9	6	66.7	0.31

several hundred kilometers during a relatively short wet climatic episode? Or are they yet to be discovered in the higher portions of the Ajo Mountains?

Comparison with previous fossil records.—The Ajo Mountains midden arthropod fauna with 53 taxa is the largest from the region and yielded 14 genera and 11 species not previously recorded in Sonoran Desert middens. These records combined with other midden faunas (Ashworth, 1976; Morgan et al., 1983; Hall et al., 1988, in press; Spilman, 1976) give a total of 102 taxa in 49 families, 57 genera, and 28 species for the region. Two species (*Niptus abtrusus* and *Onthophagus brevifrons*) and a genus (*Aphaenogastor* sp.) were previously reported from Chihuahuan Desert middens (Ashworth, 1973; Elias, 1987).

It is interesting to compare the midden arthropods from five Sonoran midden series. All samples are dominated by ground dwellers. The beetle families Bruchidae, Curculionidae, Scarabaeidae, and Tenebrionidae, Formicidae, and the genera *Argoporis* and *Pheidole* were identified from all areas. Millipedes, carabid beetles, and *Ptinus* sp. were in four faunas while *Cactopinus hubbardi, Cononotus bryanti,* and *Solenopsis aurea* were in three.

Sorenson's index of similarity was used to compare the Ajo Mountains midden fauna with the other Sonoran Desert faunas (Table 4). In this index twice the number of taxa shared between samples is divided by the sum of the taxa identified from each sample (Mueller-Dombois and Ellenberg, 1974). The index approaches one as samples become more similar. When sample sizes are disparate the indices can be artificially low.

In general the indices are similar for all of the sites except for the Butler Mountains where values are low due to small sample size. Differences between the Ajo Mountains fauna and the others probably reflect the relatively cool, wet habitats at higher elevations for the Sonoran Desert. The indices illustrate quite well that the faunas are most similar to the Ajo Mountains fauna at the family level and least at the species level. With maximum values of only 0.56 for families and 0.42 for total taxa, it is clear that there are important differences between each of the faunas as well.

The Ajo Mountains midden arthropod fauna differed from other Sonoran Desert faunas in several aspects. Millipedes were less common in Wisconsin and Holocene samples than in other areas or in Alamo Canyon today. Tenebrionid beetle remains were relatively rare throughout the Ajo Mountains sequence although 21 species were in the modern fauna (Table 3). Previous Sonoran Desert midden studies yielded three species, seven genera, and numerous indeterminate specimens. The low abundance of millipedes and tenebrionids in the Wisconsin samples may reflect their reduced abundances in mesic woodland environments compared to desertscrub habitats.

Discussion

Previous studies of midden arthropods from the Sonoran Desert have suggested that the arthropod faunas are basically conservative with fewer distributional changes than plants during late Wisconsin glacial periods with most of the arthropods potentially occurring within a few kilometers of the sites today (Hall et al., 1988, 1990). The possibility was suggested that the effects of glacial climates on arthropods decreased along latitudinal and elevational gradients with minimal changes in the Sonoran Desert lowlands. Identification of fragmentary specimens to relatively high taxonomic levels, inadequate sampling of the modern fauna, and relatively few specimens determined to species in the older samples indicated the possibility of more significant changes than detected.

The Ajo Mountains midden arthropod fauna is relatively rich (53 taxa) and from a relatively high elevation (915–975 m) in the Sonoran Desert with good middle and late Wisconsin and early Holocene coverage. Although the fauna contains quite a few arthropods that are not known from the Ajo Mountains, they are throughout the record and not just in the older samples (see above). Comparison of the arthropods and plants from the same middens in Alamo Canyon will help evaluate the relative degree of change. For the arthropods 66.7% for the middle Wisconsin (n = 12), 75.0% for the late Wisconsin (n = 32), and 83.8% for the early Holocene (n = 36) potentially (actual fossils plus likely occurrences based on other records and taxonomic levels) occur in Alamo Canyon today. Similar percentages for the plant fossils are 72.4% for the middle Wisconsin (n = 58), 75.0% for the late Wisconsin (n = 52), and 88.2% for the early Holocene (n = 68). The percentages of long-lived plants (trees, shrubs, parasites, and succulents) observed at the site and occurring somewhere in Alamo Canyon are 6.1% and 60.1% (n = 33) for the middle Wisconsin, 6.3% and 65.6% (n = 32) for the late Wisconsin, and 6.9% and 75.9% for the early Holocene (n = 29). Less change was seen in the short-lived herbaceous plants (herbaceous perennials, annuals, and grasses) with 88.0% in the middle Wisconsin (n = 25), 90% in the late Wisconsin (n = 20), and 97.4% in the early Holocene (n = 39) still in Alamo Canyon. Percentages for the plants that no longer live in the Ajo Mountains are 25.9% for the middle Wisconsin (n = 15), 23.1% for the late Wisconsin (n = 12), and 10.3% for the early Holocene (n = 7). This compares with 18.9% for the entire arthropod fauna (n = 8), 33.3% for the middle Wisconsin, and 9.4/25.0% for the late Wisconsin, and 8.1/16.2% for the actual and potential extralocals.

These percentages suggest that the differences in the responses of arthropods and plants to ice age climates were not as disparate as suggested for lower Sonoran Desert sites. The resolution in the fossil plant record is much greater allowing changes in local distributions and community structure to be observed. The plants recorded in the middens that no longer occur in the Ajo Mountains were mostly long-lived trees, shrubs, and succulents which are often the conspicuous structural dominants in the communities. The dominants apparently changed more than the arthropods or the entire flora.

Chronological development.—As discussed above, the vegetation of the Sonoran Desert has undergone a series of stages beginning with woodlands in the late Wisconsin, transitional woodland/desertscrub in the early Holocene (11,000–9000 yr B.P.), cool, wet Sonoran desertscrub in the middle Holocene (9000–4000 yr B.P.), and relatively modern desertscrub from 4000 yr B.P. until the present. Comparison of this general developmental sequence with the midden arthropods is interesting.

In the Puerto Blanco Mountains the arthropod faunal sequence began with relatively few taxa in a single late Wisconsin sample, increased gradually in the early and middle Holocene, and increased dramatically in the late Holocene paralleling the increase in subtropical plants (Hall et al., 1990). A total of 76.3% of 38 arthropod taxa appeared in the Holocene. The Holocene arthropod sequence from northwestern Sonora was similar with a major increase in species richness after 4,000 yr B.P. The midden arthropods from the Tinajas Altas and Butler mountains reflect a gradual increase in taxa from the middle Wisconsin (>43,200 yr B.P.) through the Holocene without major steps (Hall et al., 1988).

The Ajo Mountains arthropod series yielded many more taxa in the older samples. Percentages of the fauna potentially present are 60.8% in the late Wisconsin (by 14,500 yr B.P.), 66.7% in the early Holocene (9570 yr B.P.), and 70.6% in the middle Holocene (8130–8590 yr B.P.). Only 37.3% of the taxa first appeared in the Holocene. As in the other areas the greatest diversity was in the late Holocene (1150 yr B.P.) with 92.2% of the fossil taxa potentially present. As discussed above, this sample may be from a relatively short, wet period and more diverse than at other times in the late Holocene. Interestingly only 78.4% of the midden taxa potentially occur in the Ajo Mountains today while the modern fauna (Table 3) is still quite diverse.

Acknowledgments

We thank Harold J. Smith, Superintendent, and Bill Mikus, Resource Manager, Organ Pipe Cactus National Monument for their help and encouragement. Vera Markgraf, Jim I. Mead, Rebecca K. Van Devender, and Marilynn Bernzott helped with the field work. Hal Coss discovered the midden sites and collected the Alamo Canyon #3 sample. Fred G. Andrews, California Food and Agriculture Department, identified the *Akalyptoischion atrichos* specimen. Funds were provided by Southwest Parks and Monuments Association. Dana Dorner drafted the figures. Timothy L. Van Devender printed the photographs in Figure 2. Jean Morgan and Justine Collins typed the manuscript.

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